

*Reciprocal Innervation of Antagonistic Muscles. Fourteenth
Note.—On Double Reciprocal Innervation.*

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I.—Reflex excitation and inhibition when brought to play simultaneously on the motoneurons of an extensor muscle can be so balanced that there results in the muscle a contraction, the degree of which evidences algebraic summation of the two opposed influences, the inhibitory and the excitatory.* This summation is obtainable not only in the decerebrate animal but also in the purely spinal (fig. 1). In the latter it proves obtainable in preparations quite recently made spinal, for instance, after decapitation. This circumstance much facilitates the physiological study of the phenomenon. In other words, the grading (fig. 1) of reflex contraction of the extensor by varying intensity of inhibition acting along with reflex excitation can be studied in the animal freshly made spinal as well as in the animal in the decerebrate condition. The muscle which I have chiefly employed in the purely spinal preparation is the isolated extensor of the knee in the decapitated cat.

A difference does indeed exist between the reactions of the preparation in the decapitated and in the decerebrate condition. In the decapitated preparation, as in the decerebrate, the reflex effect of any inhibitory afferent is easily seen if stimulation of that afferent is employed concurrently with stimulation of an excitatory afferent. If however the inhibitory afferent is stimulated during the ordinary resting condition of the preparation, there is usually no change in the muscle to show that the inhibitory afferent is producing any effect at all (fig. 2). This is because the extensor muscle in the decapitated preparation is not exhibiting tonus and lies relaxed, therefore affording no background of contraction against which an inhibitory reflex can reveal itself by causing relaxation. Even in this condition it can, however, easily be shown that the inhibitory afferent is then really producing a state of inhibition in the preparation, although that state is not made evident by any further relaxation. If a stimulus sufficient to cause reflex contraction of the muscle be applied to the excitatory afferent while the inhibitory afferent, although apparently without effect, is being stimulated, the excitatory afferent is found to be ineffective (or only partially effective) then; but it

* Sherrington, 'Roy. Soc. Proc.,' Note XIII, Nov., 1908.

immediately becomes effective (or more effective) on withdrawal of the concurrent inhibitory stimulation (fig. 2).

Similarly with flexor muscles. The flexors of the knee can be suitably studied with *semitendinosus* or *biceps femoris*. With the latter, the posterior part only of the muscle need be used, the anterior part not being a true knee

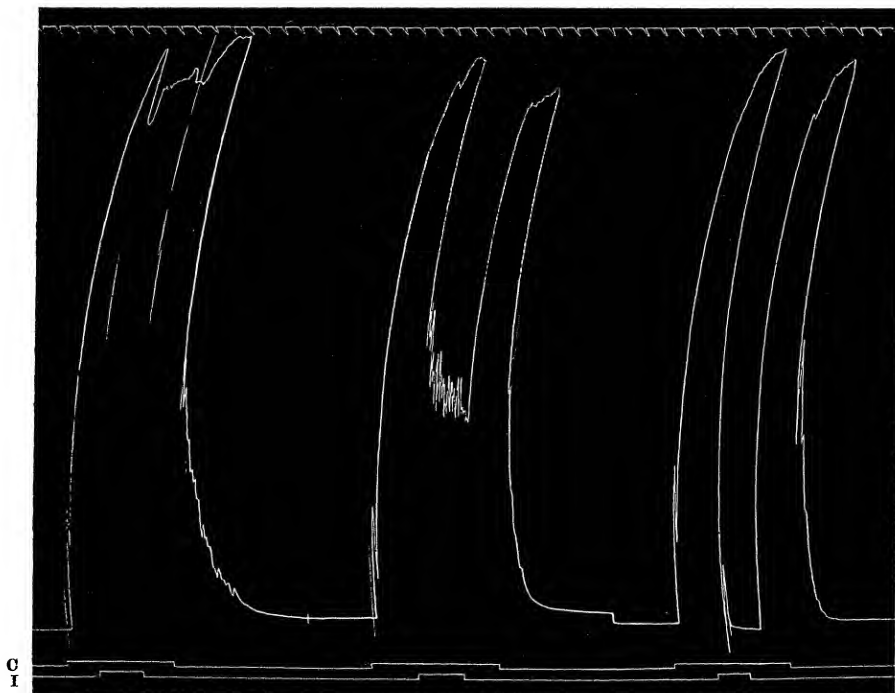


FIG. 1.—Reflex contraction of *Vastocrureus* in spinal mammal (decapitated cat), excited by faradic stimulation of contralateral popliteal nerve (C). During this contraction the ipsilateral peroneal nerve was faradised for the time shown by the lower signal (I), and produced a lessening of the reflex contraction; this inhibitory effect is greater according as the intensity of the stimulation of the ipsilateral nerve is increased. In the second observation it reduces the reflex contraction to less than half; in the third observation it suppresses it altogether for so long as the inhibitory stimulus endures. In the third observation, with the strong inhibition, so abrupt and quick is the suppression of the contraction that the writing lever gives a vibratory shake at the end of its fall. The tremor seen to occur in the second observation during the period of concurrent excitation and inhibition is usual, and is more marked in the decapitated preparation than in the decerebrate. Time in seconds above.

flexor (cat, dog). The muscle, *e.g.*, *semitendinosus*, is isolated by detachment from tibia and by severance in both hind limbs of all nerves other than its own. The reflex contraction or relaxation of the muscle can then be studied by the myograph. Reflex contraction is easily obtained by stimulation

(mechanical or electrical) of the central stump of almost any afferent nerve of the ipsilateral limb. If while this reflex contraction is in progress the central stump of a nerve, *e.g.*, popliteal, of the contralateral fellow limb be suitably faradised, there ensues immediate relaxation of the contracting semitendinosus (fig. 3). But if the contralateral afferent be stimulated while the preparation is at rest there may be no evidence of inhibition or of any other

FIG. 2.

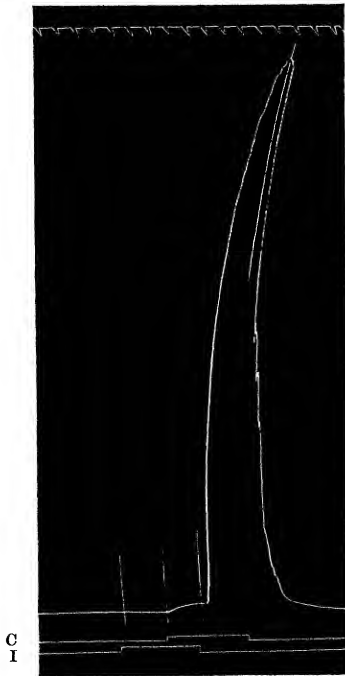


FIG. 2.—Reflex contraction of Vastocureus muscle evoked by stimulation of central end of contralateral peroneal nerve (C). Before this stimulation a stimulation of the ipsilateral peroneal (I) was commenced. This latter stimulation produced no visible effect on the muscle, but it is only on its cessation that the contralateral stimulation is able to produce a contraction. Cat, decapitated preparation. Time in seconds above.

FIG. 3.

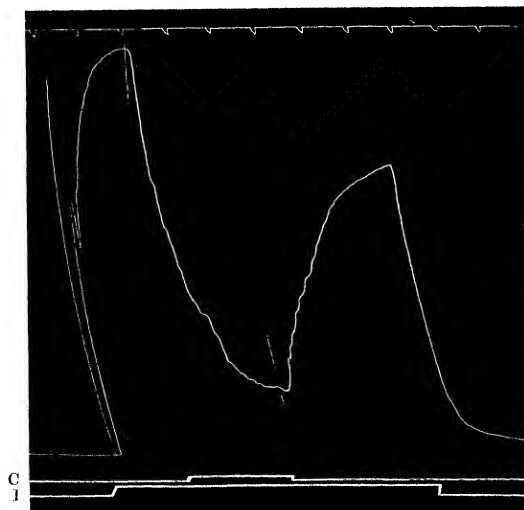


FIG. 3.—Reflex contraction of Semitendinosus, a knee-flexor, evoked by stimulation of central end of ipsilateral peroneal nerve (I), and inhibited during concurrent stimulation of contralateral popliteal nerve (C). Cat, decapitated preparation. Time in seconds above.

effect. The reflex stimulus might then be supposed not to be exerting any influence whatever on the flexor muscle. That is because there is then in the muscle no tonic or other contraction against which the reflex inhibition can show. That the reflex inhibitory influence is, however, really at work

can be shown by the same device as that employed above to reveal it under similar circumstances in the extensor muscle.

Another way in which the hidden inhibition can be revealed is by administering a small dose of strychnine. It was pointed out previously that strychnine converts reflex inhibition of the extensor and certain other muscles into reflex excitation. I find this hold good also in regard to reflex inhibition of flexors. Intravenous injection of 0.15 milligramme strychn. hydrochl. per kilogramme (cat) almost at once converts the inhibitory effect of a contralateral afferent on semitendinosus into an excitatory effect (fig. 4).

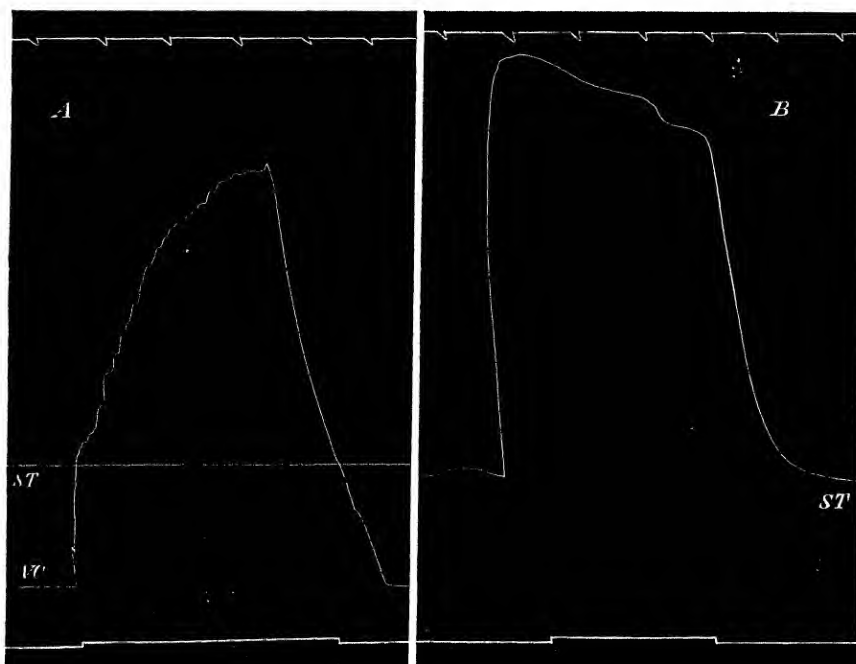


FIG. 4.—Effect of stimulation of contralateral peroneal on Semitendinosus; A, before strychnine; B, after. In B the contraction of vastocrureus is not included, but semitendinosus (ST), which had shown no contraction in A, because the stimulus was inhibitory to it, in B under the same stimulus exhibits the marked contraction shown, the small dose of strychnine having converted reflex inhibition into reflex excitation. The contraction long outlasts the period of stimulation in B.

Stimulation of the afferent then, in the resting preparation, instead of leaving the muscle apparently untouched, produces reflex contraction of it. The influence on the flexor motoneurones, which was previously unable to show itself in the relaxed muscle, because inhibitory, at once reveals its existence, because under strychnine it has become an excitatory influence.

And this holds good with the flexor muscle both in the decapitated and in the decerebrate preparation. The view that strychnine, by lessening an intracentral resistance, so allows the nervous impulse access where it previously had none, is therefore hardly applicable to the flexor any more than to the extensor: in both cases the effect is well explained by the strychnine converting reflex inhibition into reflex excitation.

II.—The algebraic summation of reflex excitatory and inhibitory effect shows itself in the flexor muscle as well as in the extensor. Suppose reflex contraction of semitendinosus to be in progress under faradisation of the central stump of an afferent nerve, *e.g.*, peroneal, of the ipsilateral limb. If then the central stump of an afferent nerve, *e.g.*, popliteal, of the contralateral fellow limb be suitably faradised, there ensues an inhibitory relaxation of the contracting muscle. When the relative intensities of the stimulations of the two nerves are appropriately adjusted, the contraction of the muscle is not wholly abolished but is merely lessened in degree. The inhibitory stimulus under these circumstances causes first a rapid partial lengthening of the muscle, indicated by a descent of the myogram line; this rapid descent reduces the contraction to a certain level of diminished contraction, which is then equably maintained during the further continuance of the inhibitory stimulus, giving a plateau in the myogram. If, then, the inhibitory stimulus be withdrawn, the excitatory still continuing as before, the reflex contraction increases again forthwith, regains a higher level, and, subject to fatigue, continues until finally the excitatory stimulus is itself withdrawn. That this grading which involves inhibition as one factor can be accomplished in either of two ways is proved by observation as follows:—Throughout a (fig. 5) consecutive series of reflexes the excitatory stimulus can be kept of constant intensity, while the inhibitory is varied in intensity in the sequent reflexes. When this is done, the amount which inhibition can subtract from the reflex contraction is found to be graduable from the hardly perceptible up to complete cancelling of all contraction for the time being. Conversely, a series of reflexes (fig. 6), in which the inhibitory stimulus remains constant in intensity but the excitatory is varied from reflex to reflex, produces degrees of reflex contraction extending from hardly perceptible lessening of the reflex contraction even to complete relaxation of the contracted muscle.

With flexor motoneurons, therefore, as with extensor, a grading of reflex contraction is obtainable by employing concurrently with reflex excitation an appropriate reflex inhibition. The algebraic summation of these two opposed influences results in an infinite series of grades of intensity of contraction both in the extensor and in the flexor muscle.

III.—The records show that the combining of any particular value of

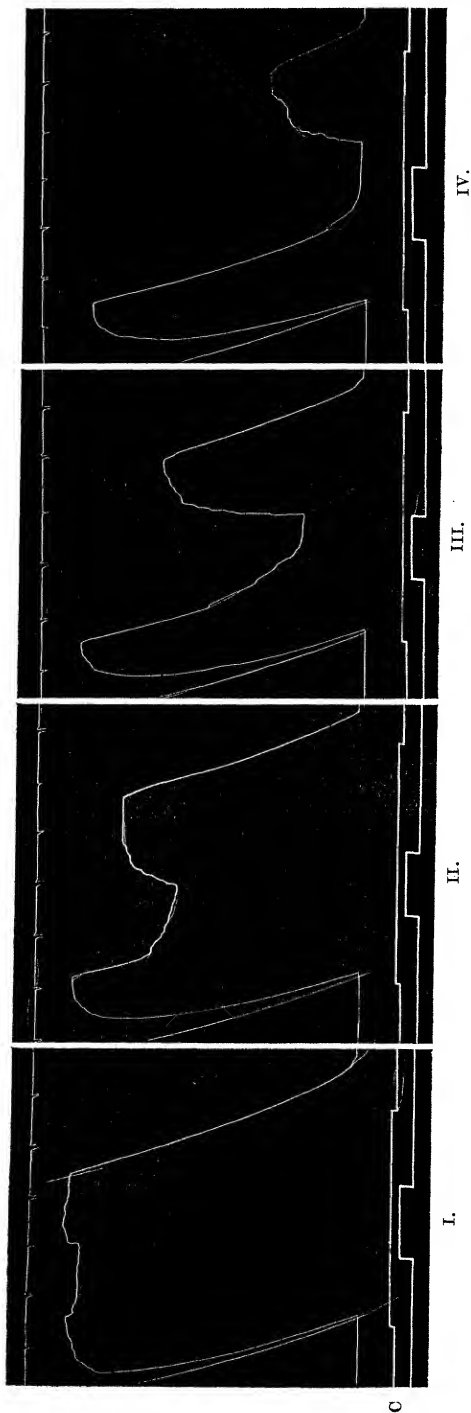


FIG. 5.—Reflex contractions of Semitendinosus evoked by stimulation of the ipsilateral peroneal (I) nerve, the intensity of this stimulus being the same throughout the four successive observations. The contraction is inhibited in each observation by an intercurrent stimulation of the contralateral popliteal nerve (C), and the intensity of this latter's stimulus is increased from observation to observation through the series. Cat, decerebrate preparation. Time in seconds above.

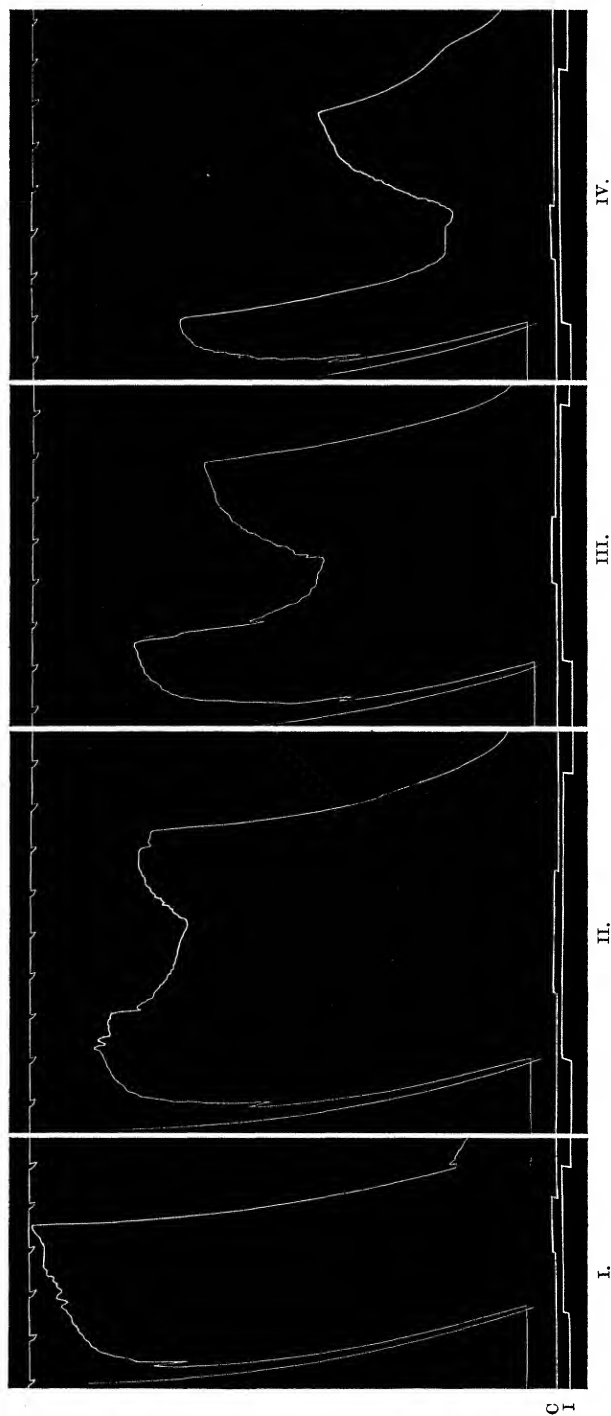


FIG. 6.—Same as fig. 5, except that the intensity of the ipsilateral stimulus (I) is varied from observation to observation, being lessened from Observation I to Observation IV progressively, while the intensity of the inhibitory stimulus (C) is kept constant throughout.

excitation with any particular value of inhibition results in a grade of contraction less than that which the excitatory stimulus without the inhibitory would give, and that this grade of contraction is fairly quickly reached, and that then this grade continues unaltered provided there is no alteration in the antagonistic stimuli. In other words, the myograph traces under the combined stimulation a plateau (figs. 5 and 6) following on a brief descent. The same plateau is seen when combined excitatory and inhibitory stimulation follows on purely inhibitory stimulation (fig. 7). This plateau indicates that under the combined stimuli a condition of equilibrium is reached, the two opposed reflex influences of excitation and inhibition balancing at a certain level of contraction or relaxation, the length of the muscle then remaining

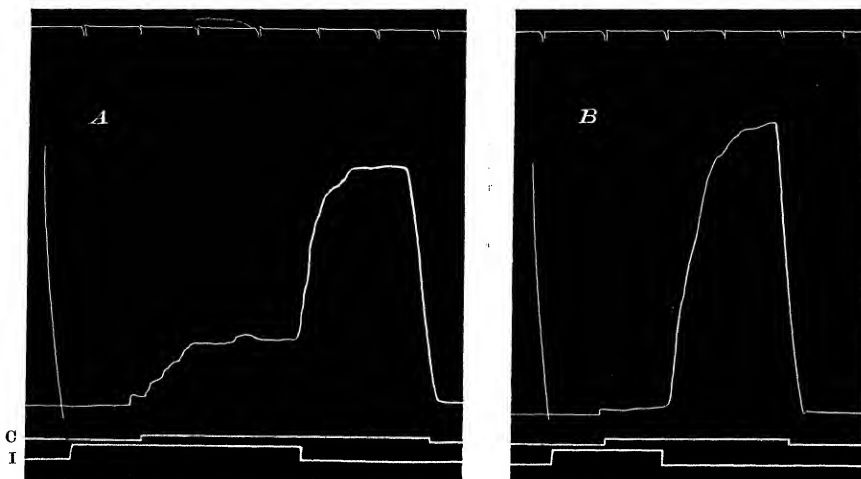


FIG. 7.—Reflex contraction of Vastocureus. The contraction is of two grades in each observation, according as there is concurrent stimulation of inhibitory and excitatory afferent, and of excitatory afferent alone. C denotes time of stimulation of contralateral peroneal nerve, I of ipsilateral peroneal. Cat, decapitated preparation. Time in seconds.

constant. This result is such as might be expected. It is a result, however, which in my experience is not obtained when reflex inhibition, however feeble, is pitted against that kind of reflex excitation which the muscle (extensor) expresses as tonus. A tonus preparation of the extensor muscle can be obtained by decerebration producing decerebrate rigidity. The relaxation caused in such a preparation by reflex inhibition progresses so long as the inhibitory stimulus continues (fig. 8). The weaker the inhibitory stimulus the slower the rate of relaxation, but the relaxing of the muscle progresses, so long as the inhibitory stimulus continues, until the full degree of relaxation and the *post-mortem* length of the muscle is gradually reached

(fig. 8). In other words, a balance between the reflex inhibition and the reflex excitation which tonus expresses is never attained.

This state of tonus appears due to a natural stimulation of mild steady quality, and in decerebrate rigidity it is, as has been shown, *autogenous* in the sense that its afferent path is constituted by proprioceptive nerve-

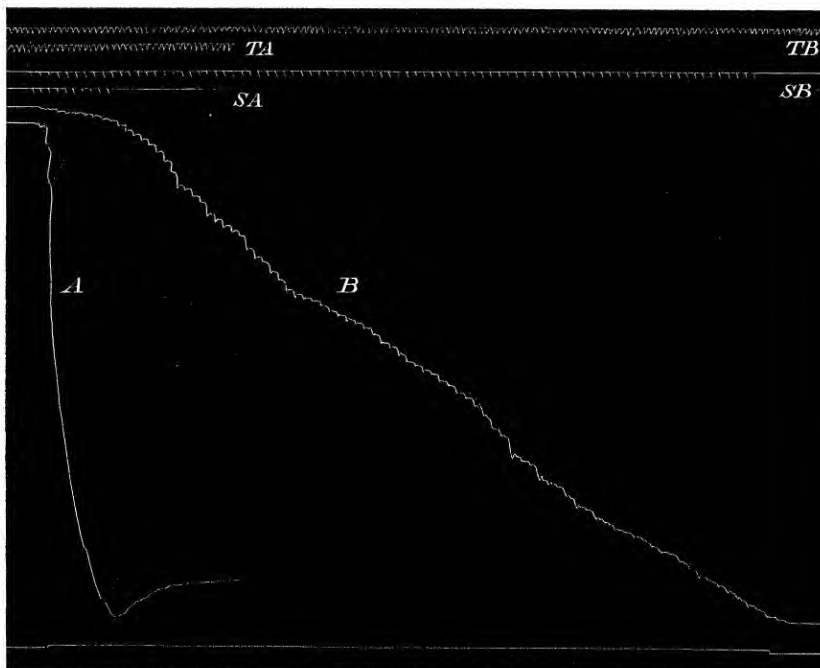


FIG. 8.—Vastocruureus preparation in Decerebrate Rigidity. Reflex inhibition is produced by stimulation of the central end of the severed ipsilateral peroneal nerve below knee, the stimulus being a series of slowly repeated break induction shocks, shown by the signal lines SA and SB. Time is marked (TA, TB) in fifths of seconds. In observation A the break-induced currents were more intense (100 units of Kronecker scale) than in observation B (20 units of Kronecker scale). Cat, decerebrate preparation. In both the observations the relaxation of the muscle proceeds to the full resting length of the muscle, but in observation A the fully relaxed condition is obtained speedily in the course of nine repetitions of the stimulus; whereas in observation B the same degree of relaxation is reached only gradually in the course of eighty-six repetitions of the (weaker) stimulus. The signal line at the foot of the figure marks the duration of the stimulation in observation B.

fibres arising in the muscle itself.* This autogenous tonus no artificial stimulus such as we apply to afferent channels experimentally for evoking reflexes has as yet succeeded in giving. The failure to exactly balance the natural reflex excitation which maintains this tonus by any artificial

* Sherrington, 'Quart. Journ. of Expt. Physiol.,' vol. 2, p. 109.

stimulation applied to inhibitory afferents may simply mean that we fail by artificial inhibitory stimuli to induce a reflex inhibition of such a kind as a natural inhibitory tonus would be, just as we fail by artificial excitatory stimuli to induce a reflex contraction of such a grade as is the natural excitatory tonus. In light of this consideration the probability appears that just as there exists a natural excitatory tonus, *e.g.*, the state of the extensors and of some adductors in decerebrate rigidity, so likewise there is a natural reflex inhibitory tonus, but that artificial stimuli such as we have at command at present fail to reproduce it. It may be that the relative slackness of the flexor muscles, in other words their exclusion from excitatory tonus, in decerebrate rigidity is the expression of an inhibitory tonus. Decerebrate rigidity is, as I have shown elsewhere,* to be regarded as a postural reflex, namely, the reflex of standing. If the flexors are under an inhibitory tonus in that reflex condition while the extensors are under an excitatory tonus, it becomes clear that reciprocal innervation applies in this static postural reflex as well as in the ordinary reflexes which execute movements and changes of posture.

In the myograph records (fig. 8) which illustrate failure to obtain balance between the natural reflex tonus of the extensor and the artificially excited reflex excitation there occurs a further feature. The rate of elongation of the tonic muscle under the weak artificially excited inhibition continues about the same from start to finish, even when the starting point is with the muscle fairly fully shortened and the end point is with the muscle fully relaxed. In other words, the degree to which the reflex inhibition over-balances the natural excitation causing the tonic contraction seems practically the same throughout. But the intensity of the stimulation of the inhibitory afferent in these observations was kept the same from start to finish; hence the inference is that the intensity of the natural reflex excitation causing the tonic contraction is about the same throughout. That is to say, the intensity of the excitatory tonus is practically the same when it keeps the extensor muscle so shortened as to maintain the knee fully extended as when the muscle under the tonus maintains the knee at an angle of *e.g.* 60°. In other words, the intensity of the reflex tonus of the extensor may be practically the same while the muscle maintains postural lengths widely different. Thus the same conclusion is reached as has been arrived at by other observations which I have published before.†

IV.—The extensor muscle of the knee (*vastocrureus*) and the flexor muscle

* 'Integrative Action of the Nervous System,' London and New York, 1906.

† Sherrington, 'Roy. Soc. Proc.,' Note XII, August, 1908; and 'Quart. Journ. of Exptl. Physiol.,' *loc. cit.*

(*e.g. semitendinosus*) of that joint being suitably isolated, the myograph can be arranged to register simultaneously the state of contraction or relaxation of both muscles. If, then, excitatory and inhibitory afferents for each of these muscles be stimulated concurrently, summation of the opposed influences of the antagonistic nerves is found to be exhibited concurrently by both muscles. The results of double (excitatory together with inhibitory) stimulation on the antagonist muscles can be grouped into cases belonging to three types. Which particular one of these three types occurs in any particular case depends on the relative intensity of the stimulation of the two afferent nerves. In my experiments usually one of the two nerves has been ipsilateral, that is, belonging to the limb to which the observed muscles belong; the other contralateral, that is, belonging to the opposite fellow limb. The ipsilateral nerve excites the knee flexor and inhibits the knee extensor (fig. 9A, Obs. I and II). The contralateral nerve excites the knee extensor and inhibits the knee flexor (fig. 9A).

Under concurrent stimulation of both ipsilateral and contralateral nerve one type of result is that the knee flexor contracts and the knee extensor is relaxed apparently fully (fig. 9B, Obs. V; fig. 11, Obs. I and II). This is the result when the stimulation of the ipsilateral afferent is strong and that of contralateral relatively weak, though yet efficient to cause contraction of extensor muscle were not the ipsilateral stimulus concurrently at work.

In a second type of case the result of the concurrent stimulation of the opposed afferents is that knee extensor contracts and knee flexor is relaxed apparently to the full (fig. 5, Obs. IV). For this result the stimulation of the contralateral afferent has to be strong and that of the ipsilateral quite weak, though strong enough to relax the extensor and contract the flexor were not the contralateral stimulus in action at the time.

In combinations belonging to the above two types, one of the antagonist muscles contracts while its opponent, if previously at rest, does not enter into contraction, or, if previously contracting, is thrown out of contraction and relaxed, exhibiting no obvious contraction either to visual inspection or in the myograph record. The result in these two types of instance, although obtained under concurrent stimulation of both afferents, resembles to outward appearance that of stimulation of either the one or the other of the antagonist afferents alone.

If, however, the relative intensity of stimulation of the two afferent nerves differs less than in the two sets of cases mentioned, the result of the concurrent stimulation of the two nerves falls out differently. In this third type of case the antagonistic muscles, flexor and extensor, both exhibit obvious contraction concurrently (fig. 9, Obs. II and IV; and fig. 10). Thus the Observation II,

FIG. 9, B.

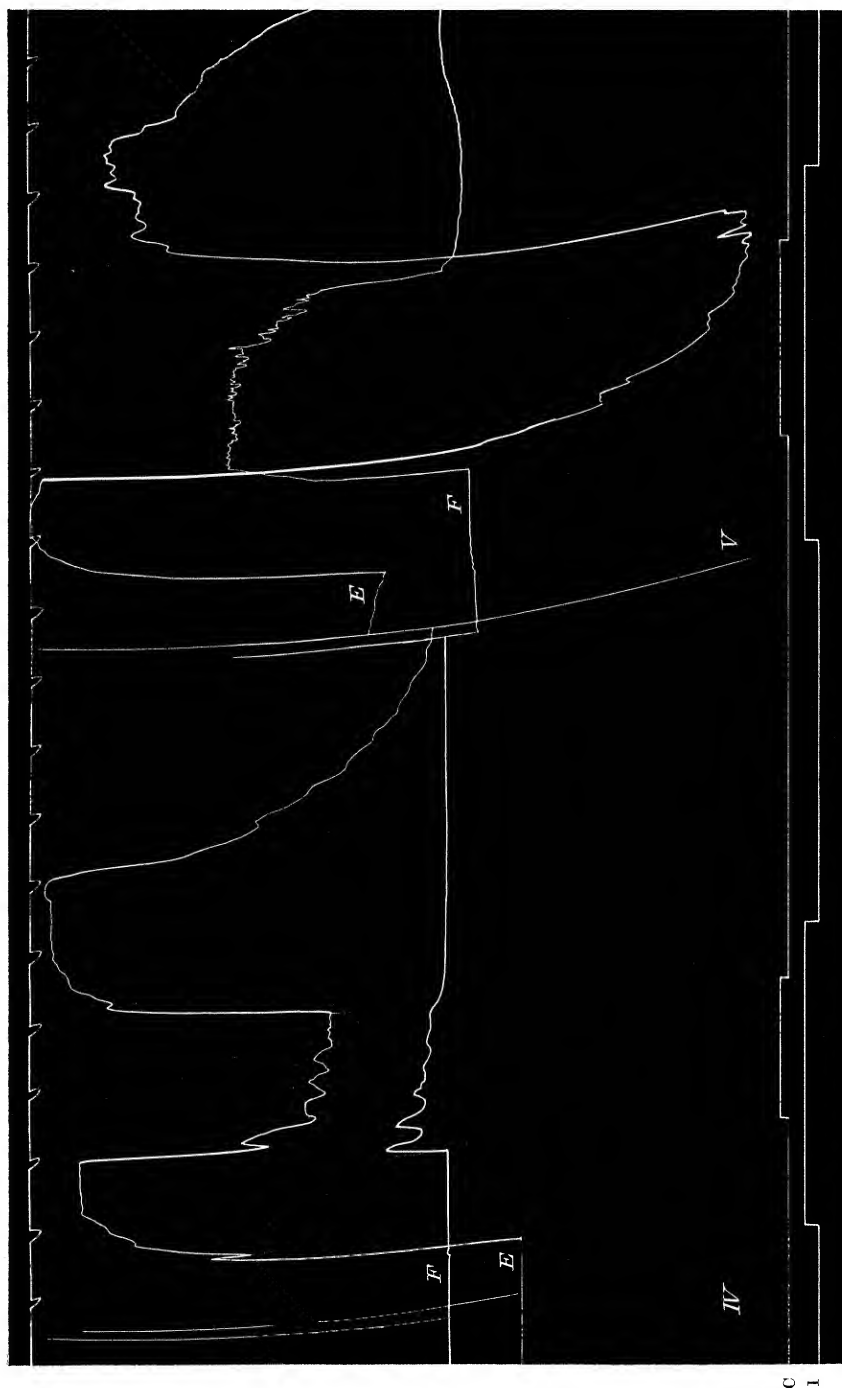


fig. 9A, opens with stimulation of the ipsilateral afferent. This causes contraction of the flexor and, at the same time, relaxation of the extensor. Some-

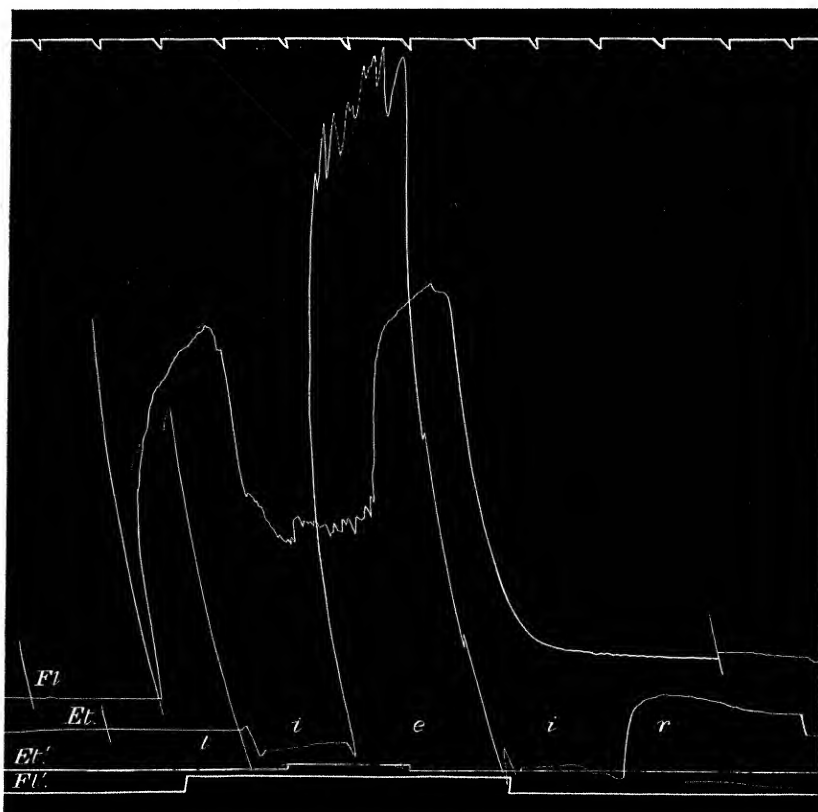


FIG. 10.—Reflex contraction of Semitendinosus, Fl, and Vastocurreus, Et, recorded with double-myograph. The lever attached to vastocurreus (Et) writes not directly below but about a centimetre to the right of that attached to semitendinosus (Fl); control arcs, cut when the recording surface was not moving, indicate the moment of commencement of stimulus on each myogram line. The ipsilateral peroneal nerve (afferent end) is stimulated as shown by the lower signal line Fl', and causes contraction of semitendinosus and relaxation of vastocurreus. Then follows stimulation of contralateral peroneal nerve as shown by the upper signal Et'. This combined stimulation lessens, but not to extinction, the contraction of semitendinosus and at the same time brings into contraction the antagonistic muscle, vastocurreus. On reverting to the single stimulation again, the contraction of semitendinosus increases once more and that of vastocurreus disappears. Finally, on cessation of the single stimulation Fl', a rebound, *r*, from inhibitory relaxation to increased tonic contraction occurs in vastocurreus synchronously with the relaxation of the flexor. Time above in seconds. Decerebrate cat.

what more than a second later stimulation of the contralateral afferent was commenced, the stimulation of the ipsilateral afferent continuing unaltered.

Under this concurrent stimulation of both nerves the extensor muscle at once contracts and the contraction of the flexor muscle continues, but in much diminished degree. About two seconds later the stimulation of the contralateral afferent is discontinued, that of the ipsilateral remaining as before. The contraction of the extensor at once dies out, and the flexor resumes the higher degree of contraction, approximately, which it exhibited before the stimulation of the contralateral nerve set in. Finally the stimulation of the ipsilateral afferent itself is withdrawn; the contraction of the flexor ceases forthwith, and the relaxed extensor then exhibits a rebound contraction, regaining its tonus, and exhibiting, indeed, a greater tonic shortening than it possessed before it was subjected at all to inhibition.* It is obvious from the record that the flexor muscle and the extensor, during the concurrent stimulation, are in contraction both of them at the same time, and that the height of contraction of the flexor is less under the twofold stimulation than under that of the ipsilateral afferent alone. That is evident not only from comparison with the flexor contraction in the first and third parts of Obs. II itself, but from comparison with Obs. I, where the behaviour of the two muscles under the stimulation of ipsilateral afferent alone with the same intensity of stimulus as in Obs. II is seen. Observations I, II, and III are successive observations taken at one minute interval. In Obs. I the ipsilateral afferent alone was stimulated, and in Obs. III the contralateral afferent alone. Returning to Obs. II, although there is clear evidence from it that the contraction of the flexor during the concurrent stimulation of the antagonist nerves is an algebraic resultant of excitation and inhibition values, what is not so evident is that the concurrent contraction of the extensor similarly exhibits an inhibitory component. That this is, however, really the case is quite clear on comparing Obs. II with Obs. III. In Obs. III the contralateral afferent alone was stimulated. This stimulation has no obvious effect on the flexor muscle (see above, Section I); on the extensor it has the effect of exciting a contraction. The intensity of stimulus applied to the nerve was unaltered from that of Obs. II. But the height of contraction evoked is much greater in Obs. III than in Obs. II. The height of contraction has, of course—this being a tonus preparation of the extensor—to be reckoned, not from the particular grade of contracted state which the tonic muscle happens to be exhibiting at the moment of excitation, but from the base line of full relaxation, such as is revealed under the inhibitions in Obs. I and II. The greater intensity of the extensor's contraction in III than in Obs. II proves that in Obs. II the extensor's contraction is less than it is under the same intensity of stimulus applied to the contralateral afferent alone and

* Sherrington, 'Roy. Soc. Proc.', Note IX, 1906.

that it is less by an amount represented by the difference between the height of contraction in Obs. II and Obs. III respectively. Comparison of Obs. II with Obs. III furnishes, therefore, one proof that under the concurrent stimulation the contraction of the extensor like that of the flexor shows algebraic summation of neural states of unlike sign. And comparison of Obs. II with Obs. IV (fig. 9B) furnishes further proof of the same thing. Obs. IV is a repetition of Obs. II, the intensities of the stimuli being the same in Obs. II, but the sequence of the stimuli in Obs. IV is in reverse order to their sequence in Obs. II. Obs. IV opens with stimulation of the contralateral afferent; this stimulation produces contraction of the extensor with no obvious effect on the flexor, the preparation not being a tonus preparation as regards the flexors. After the contralateral stimulus has been in operation for rather more than a second the ipsilateral afferent is stimulated, the stimulation of the contralateral continuing as before. The effect of the concurrent stimulation of the two nerves is that the contraction of the extensor is considerably reduced in height, and that a contraction of the flexor occurs, but this contraction of the flexor is much less than that given by the ipsilateral stimulus acting alone as in Obs. I and Obs. II. After about 2 seconds' duration the ipsilateral stimulus is withdrawn, there then ensues immediately a disappearance of the flexor's contraction and a resumption by the extensor of the full height of contraction it showed originally under contralateral stimulus alone. Finally the contralateral stimulus is withdrawn and the contraction of extensor soon begins to decline and somewhat gradually passes off. The difference between the abrupt reduction of the extensor's contraction directly the ipsilateral stimulus (inhibitory) joined the contralateral and the delayed and gradual dying out of the contraction on mere withdrawal of the exciting stimulus (contralateral) is characteristic of the difference between onset of inhibition and mere cessation of excitation in a tonus preparation.

Fig. 9B, Obs. V, taken a minute later than Obs. IV, supplies a repetition of the latter with increased strength of the ipsilateral stimulus. The result then given during the concurrent stimulation of the opposed afferents is different. The simple change in the intensity of stimulation of one of the afferents removes the result from the type 3 to type 1. Under the concurrent stimulation in this observation the flexor contracts while simultaneously the contraction of the extensor is apparently completely suppressed, whereas under the concurrent stimulation in Obs. II and IV both the flexor and extensor are synchronously in active contraction.

In this third type (fig. 9, Obs. II, Obs. IV, and fig. 10) of result, therefore, concurrent stimulation of the two antagonistic afferents produces

in the antagonistic muscles obvious contraction concurrently in both. But though both the muscles are contracting the contraction of each is seen to be less than it would be were there not then in action the reflex which produces contraction of its antagonist. And this is so because some reflex inhibition of the motoneurons of each accompanies the reflex excitation of the motoneurons of the other. Thus the contraction of semitendinosus is less than it would be were not the contralateral afferent being concurrently stimulated, and the contraction of vastocrureus is less than if the ipsilateral afferent were not concurrently stimulated. As to which of the two antagonists exhibits the greater contraction, that feature is determined by the relative intensity of the stimulation of the two antagonistic afferents. To obtain the type 3 of result the effects of the two opposed afferents have, of course, to be sufficiently nearly balanced, and the intensity of the one must not wholly overbalance that of the other. Within these limits, however, all degrees of grading of combination of the two seem obtainable by simple adjustment of the relative intensity of the stimulation of the opposed nerves. In short, a delicate grading of the intensity of contraction is effected by bringing into play a double reciprocal innervation. The result of the double reciprocal action is that each of the two muscles displays simultaneously with its antagonist an algebraic summation of reflex inhibition and reflex excitation. In other words, antagonistic reflexes add themselves algebraically with unlike signs.

To obtain this result with spinal reflexes, *e.g.* in the decapitated mammal, or with reflexes produced by stimulation of afferent nerves in the decerebrate animal, it is necessary to stimulate synchronously two or more afferents of opposed effect as regards the antagonist muscles selected. Stimulation of either of such opposed afferents taken alone never suffices, in my experience, to produce simultaneous contraction, *e.g.* of the knee flexor and extensor. In short, concurrent contraction of the antagonists denotes that two antagonistic reflexes are synchronously at work and are operating with intensities not far removed from balancing one another. In this respect there is a significant resemblance between spinal reflex co-ordination and that exercised by the motor *cortex cerebri*. Electric stimulation at one cortical point giving contraction of, *e.g.* flexor of elbow with relaxation of the antagonist extensor, and stimulation at another cortical point giving contraction of the antagonist extensor with relaxation of the flexor, synchronous stimulation of the two cortical points together does often, I find, give, if suitably graded, a concurrent contraction of both flexor and antagonist extensor together.

V.—Apart from the intensity of the stimuli applied to the opposed afferent

nerve there is, however, another factor controlling the balance of reflex result on the antagonistic muscles. It was shown previously that the ipsilateral reflex on the knee muscles is, as compared with the crossed reflex, the prepotent one. Remembering that the influence of the ipsilateral afferent is excitation of the flexor and inhibition of the extensor, while that of the contralateral afferent is inhibition of the flexor and excitation of the extensor, it has been shown that each of these afferent nerves can be made to preponderate in reflex result over the other. This preponderance in effect of the one over the other can be impressed on either the one or the other of the two by simply stressing the intensity of the stimulus to the one it is desired should preponderate. But it is less easy to secure prepotency for the contralateral nerve than for the ipsilateral. The ipsilateral reflex seems to function with an inherent greater intensity than the contralateral. Fig. 11.

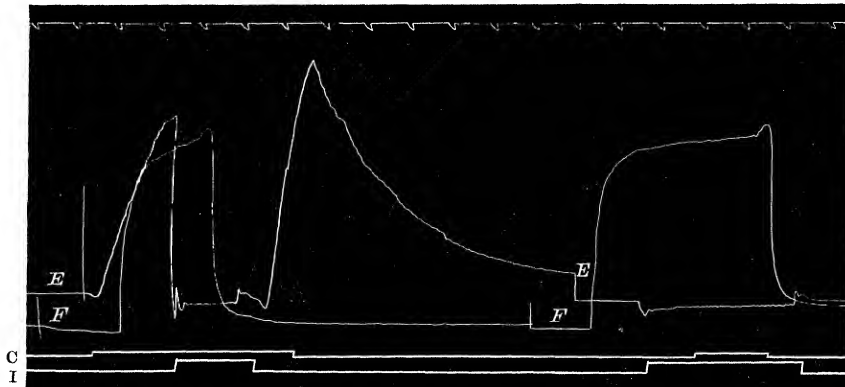


FIG. 11.—Double-myograph Observation. E marks vastocruureus, F semitendinosus, C contralateral stimulus, I ipsilateral stimulus. Cat, decerebrate preparation. Time in seconds. Description in text. The myograph lever attached to vastocruureus writes not directly above that attached to semitendinosus, but about a half centimetre to right of it; arcs cut by the levers on the recording surface when stationary mark the moment of application of stimulus on each myograph line.

exemplifies the effect that this has on the experimental adjustment of the stimuli required for algebraic summation of excitation and inhibition. The observation opens with stimulation of the contralateral afferent which produces contraction of the extensor muscle and no obvious effect on the flexor, the preparation not being a tonus preparation as regards the flexor. Two seconds later there ensues stimulation of the ipsilateral afferent, stimulation of the contralateral continuing unaltered; the flexor at once contracts, and the contracting extensor is at once relaxed, and so speedily and fully that its lever gives a vibratory shake after the fall. A second and a half later the ipsilateral stimulus is withdrawn; the contraction of the flexor then dies off, and the contraction of extensor reappears and regains its

old prominence. Finally, the contralateral stimulus is withdrawn and the extensor's contraction gradually passes away. After a minute's pause the observation was repeated with unaltered intensity of the stimuli, but with reversal of their sequence. The ipsilateral stimulus precedes and produces its unopposed effect; this stimulus still remaining in operation, the contralateral stimulus is now combined with it and remains without visible influence on the myogram, although what its unopposed effect would be is guaranteed by the just preceding observation. This comparatively easier suppression of the contralateral reflex by the ipsilateral than of the ipsilateral by the contralateral explains how it is that when similar afferent nerves of both hind limbs or similar points of skin in the limbs are simultaneously and similarly stimulated extension occurs in neither limb and flexion occurs in both.*

The effect of fairly strong and equal concurrent stimulation of symmetrical afferents of the two limbs in giving flexor effect at both knees, whereas stimulation of one of the afferents gives flexion at ipsilateral knee and extension at contralateral, recalls strikingly a result obtained by Mott and Schäfer† on the eyeball movements under concurrent stimulation of balanced points of the two cerebral hemispheres right with left. Stimulation of the cortex of one hemisphere gives lateral deviation of both globi to the opposite side. It has been shown‡ that in this movement reciprocal innervation is at work producing inhibition of one muscle with excitation of its antagonist. Mott and Schäfer found concurrent stimulation of points in the two hemispheres produce, when appropriately graded, a convergence of the two globi. Here, obviously, of the two antagonistic influences, that on the ipsilateral globus preponderates over that on the contralateral, just as in the case of the limbs the ipsilateral reflex preponderates over its antagonistic contralateral. And in the eyeball result, just as in the result on the limbs, I imagine that appropriate analysis would reveal in this case an algebraic summation of excitation and inhibition just as with the flexor and extensor knee muscles. In short, in both cases antagonistic reactions are adding themselves with *plus* and *minus* signs.

VI.—It will be noted that the ipsilateral afferent, just as it is prepotent in excitation, so also is prepotent in inhibition. This supports the view put forward in these Notes§ that the inhibition and the excitation are complementary

* Sherrington, article "Spinal Cord," 'Schäfer's Text-book of Physiology,' vol. 2, p. 840, 1899; also 'Integrative Action of Nervous System,' p. 225, 1906.

† 'Brain,' vol. 13, p. 170, 1894.

‡ Sherrington, 'Roy. Soc. Proc.,' Note II, vol. 53, p. 411, 1893.

§ Sherrington, 'Roy. Soc. Proc.,' Note VIII, vol. B 76, p. 277, 1905.

parts of one and the same reflex. In harmony with this stands also the fact that when the one or the other afferent is made prepotent by suitably increasing the intensity of its stimulus, the prepotency obtains both for excitatory influence and inhibitory influence alike. The reflex produced by either afferent is, in fact, a reflex of simultaneous double sign ($\pm$ reflex). And in the observations furnished there is a good deal of evidence suggesting that the relation between the intensity of the excitatory part of the reflex and the inhibitory is such that the intensity of the one increases proportionally with that of the other. The rhythm of the inhibitory effect in the motoneurons of one muscle appears also to be synchronous with that of the excitatory effect in the motoneurons of the antagonist muscle, to judge by the rhythmic tremor not unfrequently evident on the myograph tracings. Observation IV of fig. 9B furnishes an illustration of this.

VII.—It was shown previously that after reflex inhibition of the motoneurons of the extensor muscle there ensues, in decerebrate rigidity, on withdrawal of the inhibitory stimulus, a contraction of the muscle. This is the rebound contraction which I attribute to “successive spinal induction.” It may far exceed in intensity the tonic contraction which existed prior to the inhibition. The question arises as to what state obtains in the flexor muscle when this rebound contraction of its antagonist occurs. With the double myograph recording both extensor and flexor simultaneously, this relation can be studied. Fig. 9A, Obs. I and II, and fig. 10, *r*, give instances of the time relations observable. On withdrawal of the ipsilateral stimulus, the flexor contraction passes off, and at the same time there takes place the rebound contraction of the extensor. Often a relatively long latency period intervenes between the cessation of the stimulus and the onset of the extensor’s rebound contraction. Similarly it is not unusual for the contraction of the flexor to outlive the duration of the excitatory stimulus for a certain time, the flexor motoneurons exhibiting after discharge. The simultaneous record of the two muscles shows that the rebound contraction of extensor synchronises with the dying out of the after-contraction of the flexor; the after discharge (rebound) of the extensor motoneurons comes into action as that of the flexor motoneurons passes off. Therefore, in the after-action shown by these antagonistic centres, there is evident the same kind of reciprocal activity as is seen in their reaction under stimuli in application at the time. In after-discharge and in tonus, as also when reacting to ordinary reflex stimulation, reciprocal innervation seems to hold good in regard to the mutual relation between the motor centres of the antagonistic muscles.
